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OBSERVATIONS ON *HIPPONIX ANTIQUATUS* (Linnaeus)*

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Introduction

One of the most interesting of the commoner gastropods found on the shores of California is the small *Hipponix antiquatus.* It is a member of one of the many groups of limpets which have independently been evolved, but it is of particular interest owing to its sedentary habits. While it must move about in early life, at some stage, at present unknown, *H. antiquatus* settles permanently. It then proceeds to lay down calcareous matter on the surface of the underlying rock. This cemented "ventral valve" may eventually attain much the same size and thickness as the true shell. *Hipponix* may be described as a univalve which converts itself into a bivalve, but it should be noted that the valves are dorsal and ventral, resembling those of a brachiopod, not those of a lamellibranch.

Despite their interesting habits little seems to have been written about these animals. The only paper found which deals with habits is one on *H. australis.* This species lives usually on the shells of species of *Turbo* and was studied at New Caledonia by Risbec (1935). The opportunity was taken while visiting professor in the University of California in 1949 to examine, first at Berkeley and later at Pacific Grove, living specimens

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*Being "Studies on Pacific Coast Mollusks, VII" (nos. I-VI, published in University of California Publications in Zoology, vol. 55, pp. 395-454).

of *H. antiquatus* which were obtained from Moss Beach, a little south of San Francisco, and from the shores of the Monterey Peninsula. In view of previous work on feeding in the allied *Capulus ungaricus* (Yonge, 1938) and on the pallial organs in other limpets (Yonge, 1947), special attention was paid to the mode of feeding and to the nature and mode of functioning of the organs in the mantle cavity. Some specimens were fixed in Bouin's fluid and were later sectioned, or mounted entire, in the Department of Zoology, University of Glasgow. But this paper deals primarily with observations on the living animal and no attempt has been made to give a detailed description of structure.

This work was made possible by the kind cooperation of colleagues in the Department of Zoology, University of California, Berkeley, and of Dr. R. L. Bolin and members of the staff of the Hopkins Marine Station, Pacific Grove. At Glasgow, Dr. H. F. Steedman gave great help by preparing whole mounts and cutting sections.

Appearance and Habits

Hipponix antiquatus is the commonest of several species of its genus recorded from the coast of California (Keep and Bailey, 1935; Smith and Gordon, 1948). It ranges from south of the equator to about 42° N. latitude (Keen, 1937). It has a rounded, much flattened shell. As shown in figure **1A**, the apex is not central but lies well to the posterior side, and the outer surface is grooved. The transverse diameter of the shell is usually a little greater than the antero-posterior diameter, the specimen shown in figure 1 being 1.7 cm. by 1.6 cm. No larger specimen was found and it was also unusually regular in shape, many shells being distorted owing to the confined space in which the animal had originally settled.

The shell is smooth internally and the impression of the horseshoe-shaped shell muscle is clearly marked on the surface of both the shell and of the "ventral valve" below (fig. **1B** and **C**). The latter is formed by the epithelium of the under surface of the foot and in the same way as the shell, i.e., the pedal margins increase it in extent while it is continually being thickened by secretion from the general surface of the foot. Eventually it comes to have much the same maximum thickness as the shell, about 1 mm. It is internally concave and to about the same depth, in this case some 4 mm., as the shell (cf. fig. **1B** and **C**). The only difference between the two is that the greatest depth in the "ventral valve" is central and not posterior as it is in the shell.

Smith and Gordon (1948) state that this species occurs "In colonies under rocks at low tide; common." It was sought with greatest success in narrow, often overhung, crannies in the rock from mid-tidal levels and

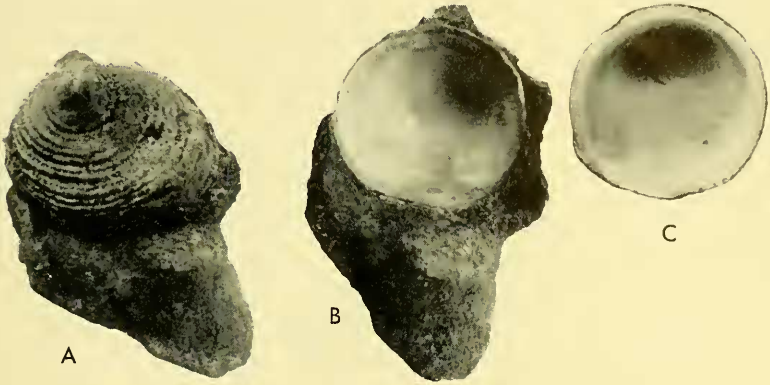

Figure 1. *Hipponix antiquatus*, photographs of shell. ×1½. **A**, shell *in situ* on rock; **B**, interior of "ventral valve" secreted by ventral surface of foot, scars of shell muscle shown; **C**, interior of "dorsal valve," i.e. true shell secreted by mantle, scars of shell muscle shown.

below. It is there protected from the full force of the Pacific surf while the movements of these waters continually bring in new supplies of organic debris and detritus of all kinds. The animals always appear to occupy rounded depressions in the rock surface. These have frequently, if not always, been made initially by rock-boring bivalves, which are extremely numerous in this rock. It is possible, however, that the depression may be further excavated during growth, presumably by means of the shell margins. But this process must cease as soon as calcareous material begins to be secreted ventrally.

VENTRAL ASPECT

The appearance of an animal after careful removal from the rock by cutting through the attachments to the cemented "ventral valve" is shown in figure 2, the specimen being viewed to some extent from the anterior end so as to obtain a better view of the head and the more anterior organs in the mantle cavity. Like the majority of limpets, e.g., both the archaeogastropod Patellacea (Docoglossa) and the pulmonate *Siphonaria* (Yonge, 1947, 1952), the shell muscles (SM) unite posteriorly although in *Hipponix* the connexion is very narrow. Laterally, however, the muscles are very broad and they provide extensive attachment between the upper and lower "valves." Contraction pulls the shell firmly against the "ventral valve" and, as this has been laid down while subject to the constraining influence of the shell, it follows that the margins of the two "valves" make perfect contact. This ensures protec-

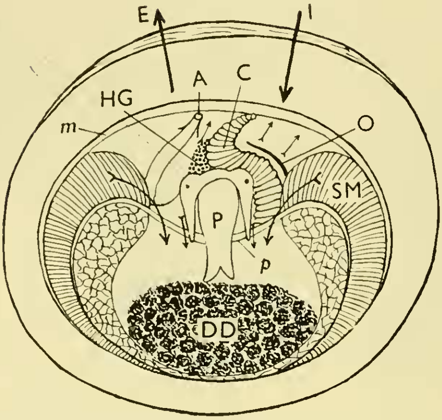

Figure 2. *Hipponix antiquatus*, appearance in life, viewed from antero-ventral aspect. ×5. *A*, anus; *C*, ctenidium; *DD*, digestive diverticula; *E*, exhalant current; *HG*, hypobranchial gland; *I*, inhalant current; *O*, osphradium; *P*, proboscis; *SM*, shell muscle; *m*, *p*, anterior margins of mantle and of foot, forming dorsal and ventral surfaces of mantle cavity. Feathered arrows indicate direction of cleansing currents.

tion against enemies and also against the force of the sea and the danger of desiccation. But it has only been achieved at the expense of mobility. The various "homing" limpets, e.g., species of such very widely separated genera as *Patella* and *Siphonaria*, have retained the power of locomotion and yet achieved an equal measure of protection because the margins of the shell make perfect contact with the rock surface of the "home."

The mantle cavity is bounded dorsally by the mantle (*m*) but ventrally by the membranous extent of the foot (*p*) which stretches forward between the shell muscles which form the lateral walls of the cavity (see also fig. 5). The head may project out of the mantle cavity, as it is shown doing in figure 2, but can be withdrawn into this by contraction of asymmetrical retractors (figs. 4 and 7; LR, RR). The head extends into a conspicuous proboscis (P) which is flanked by a pair of stout tentacles each with a small eye on the dorsal surface near to the base.

Foot

The characteristically sessile habit of the adult of *Hipponix* is associated with major modifications of the foot. While, as in all limpets, the shell muscles are very large, the central region of the foot, which in other limpets forms the greater part of the creeping sole, is here devoid of muscle. It consists solely of a thin membrane much of which forms the floor of the mantle cavity. This is best indicated by the sections shown in figures 5 and 7. The ventral surface of the foot extends peripherally so that it covers the same area ventrally as the mantle does dorsally and its epithelium has a similar capacity for secreting shell. It is as though the animal had two mantle lobes, dorsal and ventral, but nowhere connected. Secretion of calcareous matter by the pedal epithelium may possibly represent some elaboration of the original powers of mucous production. The "ventral valve" so formed is cemented firmly to the underlying rock. As noted above, the shell muscles serve as adductors drawing the free "dorsal valve" tightly against the attached "ventral valve."

At the base of the proboscis ventrally there is a small flap of tissue which projects forward from the mesopodial tissue below. This is the propodium (figs. 4, 5 and **7A**; PR); it is terminally notched and a small gland opens on its dorsal surface. It appears to be concerned solely with attachment of the egg capsules in which connexion it will be mentioned again later.

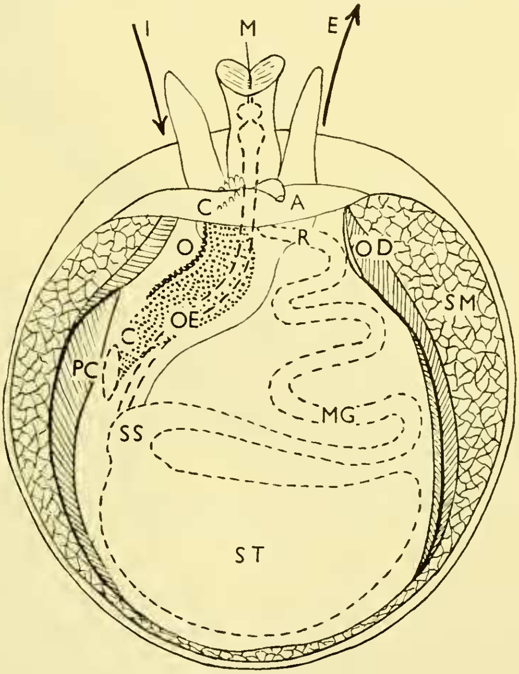

Figure 3. *Hipponix antiquatus*, dorsal view after removed from shell, based on examination of living animals and of dissections; course of alimentary canal indicated by broken lines. ×5. *C—C*, extent of ctenidium (dotted where viewed through the mantle wall); *M*, mouth; *MG*, mid-gut; *OD*, opening of oviduct; *OE*, oesophagus; *PC*, pericardium; *R*, rectum; *SS*, style-sac; *ST*, stomach. Other lettering as before.

Mantle Cavity

After removal from the shell, the animal may be viewed from the dorsal aspect, as shown in figure 3. Owing to the forward extension of the shell muscles and the consequent constriction of the opening of the mantle cavity, the anus (A) has been displaced dorsally, opening slightly to the right of the mid-line. The anterior end of the ctenidium (C) is similarly carried round dorsally, terminating just to the left of the anus.

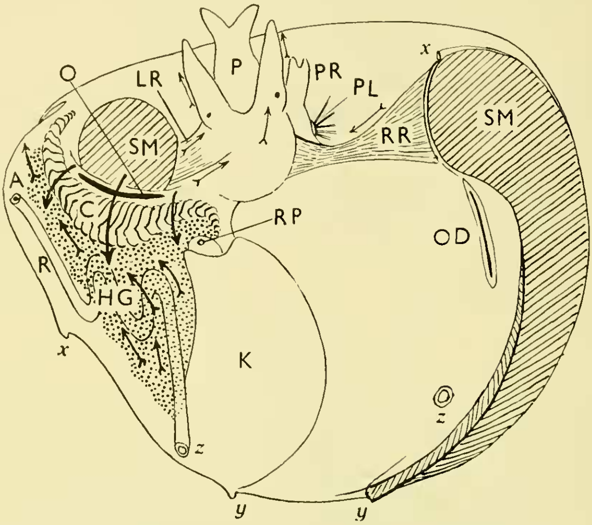

Figure 4. *Hipponix antiquatus*, dorsal view of organs in the mantle cavity after opening along the right side. ×5. *K*, kidney; *LR*, left retractor muscle of head; *PL*, plate where egg capsules (stalks only shown) are attached; *PR*, propodium; *RP*, renal pore; *RR*, right retractor muscle of head. *x—x*, cut ends of mantle edge; *y—y*, cut surfaces, posterior wall of mantle; *z—z*, cut ends of mid-gut. Other lettering as before. Plain arrows indicate respiratory current between ctenidial filaments, feathered arrows cleansing currents.

The mantle cavity can best be examined after cutting along the edge of the shell muscle on the right side and then turning the roof of the mantle cavity over to the left, giving the appearance shown in figure 4. The point of immediate interest is the asymmetry due to dorso-ventral compression in *Hipponix*. In archaeogastropod limpets, such as *Acmaea* or *Patella* (Yonge, 1947), and also in the mesogastropod *Capulus*, which is closely related to *Hipponix*, the head occupies the center of the mantle cavity. This is a consequence of secondary symmetry associated with loss of coiling in the shell and visceral mass. In all of these limpets height is seldom less than breadth, it is often greater. In *Hipponix*, on the other hand, height is always less than half the breadth. As a result of this and of the reduction of the pedal tissues (with which this compression is also associated), the mantle cavity extends relatively far back, as shown in longitudinal section in figure 5. But it also widens out internally and is very shallow. Hence the head, although it projects forward out of the middle of the opening of the mantle cavity (figs. 2 and 3), has basally been pushed over to the left (figs. 3 and 7) where the oesophagus (OE) runs into the visceral mass This accounts for the much greater size of the right as compared with the left retractor muscle of the head (figs. 4 and **7B**; RR, LR).

Apart from this flattening and extension posteriorly, the mantle cavity is that of a typical pectinibranch prosobranch, having the same general disposition of the pallial organs as, for instance, in *Buccinum* (Yonge, 1938). The pericardium, as revealed by dissection and in sections, is situated far to the left at the base of the ctenidium (figs. 3 and **7C**; PC). The large kidney (fig. 4, K) covers much of the posterior wall of the mantle cavity, the renal pore (RP) opening to the left of the mid-line. Internally it is unusually capacious, as shown in figure 5. It communicates with the pericardium by way of a long reno-pericardial canal (figs. 5 and **7C**; RC). On the right side of the cavity extends the elongated genital aperture which, in all the specimens that were dissected, was oviducal (figs. 3 and 4 OD). The rectum (R) meanders along the right side of the roof of the cavity to open, near the margin of this, at the anus (A). The large pectinibranch ctenidium (C) occupies the left side of the mantle cavity twisting over to the dorsal surface anteriorly as mentioned above. Parallel to its axis on the left and so facing the inhalant current (fig. 3, I) extends the linear osphradium (figs. 3; 4;

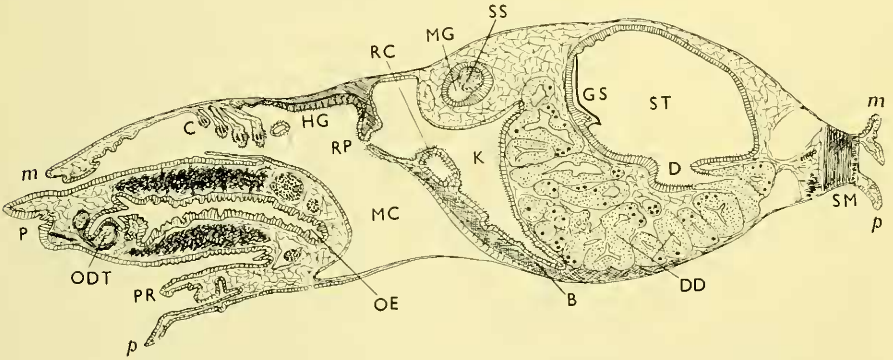

Figure 5. *Hipponix antiquatus*. longitudinal section. ×11. *B*. blood sinus; *D*. duct into digestive diverticula; *GS*. gastric shield; *K*. internal cavity of kidney; *MC*. mantle cavity; *ODT*. odontophore cartilage; *RC*. reno-pericardial canal; *SS*. style-sac with contained style. Other lettering as before.

and **7A**, O). Between the ctenidium and the rectum, the roof of the cavity is covered by the extensive tissues of the hypobranchial gland (figs. 4; 5; and 7, HG).

Ciliary Currents

The lateral cilia on the ctenidial filaments create an inhalant current (I) which enters the cavity on the left side, impinging first on the osphradium. The exhalant current, as always, leaves the cavity on the right. The ctenidium is concerned solely with creating this current and with respiratory exchange. As shown in figure 4, the filaments are broad, like those of a typical pectinibranch. Where the filaments are modified in connexion with ciliary feeding, they are invariably elongated, e.g. in *Vermetus novae-hollandiae*, *Capulus ungaricus* and, to a striking extent, *Crepidula fornicata* (Orton, 1912, Yonge, 1938). This elongation increases both lateral and frontal surfaces and so the extent of the lateral cilia, which create a greater inhalant current, and of the frontal cilia which are here concerned with food collection. In *Hipponix* there is only a moderate inhalant current, adequate for the limited respiratory needs of the animal, while the frontal cilia retain their primitive function of cleansing.

In ciliary feeding species, moreover, collected particles are conveyed to the mouth along the tips of the elongated filaments, and by way of special food grooves, to the mouth. This has been described in various of the Vermetidae (Yonge, 1932, 1938; Morton 1951*b*), in *Turritella communis* (Graham, 1938), in the Struthiolariidae (Morton, 1951*a*)—although *not* in the related *Aporrhais* which has the same habit of burrowing in mud (Yonge, 1937)—in *Crepidula* and other members of the Calyptraeidae (Orton, 1912, Yonge, 1938), in *Capulus ungaricus* (Yonge, 1938), and in the freshwater *Viviparus viviparus* (Cook, 1949).

Careful observation in *Hipponix* showed that there is no passage of particles along the tips of the filaments or within a food groove to the mouth. The circulation of water and the disposal of waste particles in the mantle cavity is essentially as in typical pectinibranchs. As described elsewhere (Yonge, 1938), there are three currents concerned with rejection of sediment, (*A*) those carrying heavier particles to the *inhalant* opening; (*B*) those carrying medium particles across the *floor* of the mantle cavity; (*C*) those carrying the finest particles over and between the ctenidial filaments for later consolidation *dorsally* in the mucus from the hypobranchial gland. Material in currents *B* and *C* is passed out through the exhalant aperture. The feeding currents in ciliary feeding Prosobranchia represent modifications of some or all of these currents (Yonge, 1938).

In *Hipponix* the only modification is due to the constriction of the opening of the mantle cavity which has had the effect of carrying the greater part of the ctenidium on to the dorsal surface so that, as shown in figures 2 and 7, the filaments hang down above the head. The inhalant current (I) created by the lateral cilia enters on the left side, passes through the ctenidium and leaves as an exhalant current (E) on the right (fig. 3). The heaviest particles drop out of suspension on the left and are removed by cilia of current *A* on the floor of the inhalant aperture (fig. 2). The current then impinges on the osphradium (O) and passes between the filaments. Larger particles are carried to the tip of the filaments by the frontal cilia and are rejected by cilia on the surface of the head, on the sides of the tentacles and on the floor of the mantle cavity to the right, that is current *B* (fig. 4). The finest particles are carried between the filaments and are then consolidated in the mucus from the hypobranchial gland. Cilia of current *C* then carry the mucus-laden masses to the exterior. The large size of the hypobranchial gland indicates the amount of material carried normally in suspension. Observations in life revealed great quantities of mucus in the mantle cavity. Posterior to the line of the right retractor of the head, the floor of the mantle cavity is not ciliated. No doubt any material which may accumulate here is forced out when the shell muscles contract.

It was initially most surprising to find no trace of ciliary feeding in this sedentary animal. The Vermetidae, which are also cemented, feed either by ciliary currents or by mucus strings (Yonge, 1932, 1938; Yonge and Iles, 1939; Morton, 1951*b*) while *Capulus ungaricus*, which is closely related to *Hipponix* and still potentially, if seldom actually, mobile is a ciliary feeder (Yonge, 1938). In that species particles collected by the ctenidia are carried in a ciliary tract to the upper surface of the propodium (much larger than that of *Hipponix*) where the proboscis collects the mucus-laden masses by means of the radula. Orton (1949) has pointed out that *Capulus* may also live on the shells of lamellibranchs, such as *Modiolus* and *Monia*, and probably takes some of the food of these animals by inserting the proboscis into the mantle cavity. But in *Hipponix* there is no doubt that ctenidium and ciliary rejection currents are in no way modified for feeding.

The presence of a large osphradium is interesting. If this organ be solely chemo-receptive then its persistence in a sedentary animal is surprising. On the other hand if, as suggested elsewhere (Yonge, 1947), it is, at least primarily, a tactile organ concerned with estimating the amount of sediment carried in with the inhalant current, then its retention would be expected. A sedentary animal is particularly susceptible to danger from accumulation of sediment within the mantle cavity.

Alimentary Canal

The mouth consists of a vertical slit at the end of the proboscis and at the base of the two lateral flaps in which this terminates. There is a small, and certainly functional, radula and small salivary glands. The buccal cavity leads into what is termed by Graham (1939) the anterior oesophagus and which possesses in *Hipponix* a dorsal ciliated food-channel of unusual width. As in other style-bearing mesogastropods, such as *Capulus* and members of the Calyptraeidae, the lateral glandular pouches primitively associated with the mid-oesophagus (Graham, 1939) are absent in *Hipponix*. As already noted, the oesophagus passes to the left to enter the visceral mass; there it enters the exceptionally large stomach (ST) which, as shown in figures 3 and 5, occupies the greater part of the posterior region of the visceral mass.

The general appearance of this organ when opened mid-dorsally is shown in figure 6. The oesophagus (OE) enters ventrally on the left side; the mid-gut (MG) which is separated by a conspicuous typhlosole (TY) from an associated style-sac (SS), leaves on the same side but dorsally (fig. 3). There is a common opening, on the floor of the stomach, for all the ducts of the digestive diverticula (figs. 5 and 6; D). This opening lies near to the gastric shield (GS) against which the short style bears. All of these structures lie on the left side of the stomach together with the usual sorting mechanisms of ridges and grooves, all richly ciliated. But some three quarters of the stomach consists of a capacious caecum which

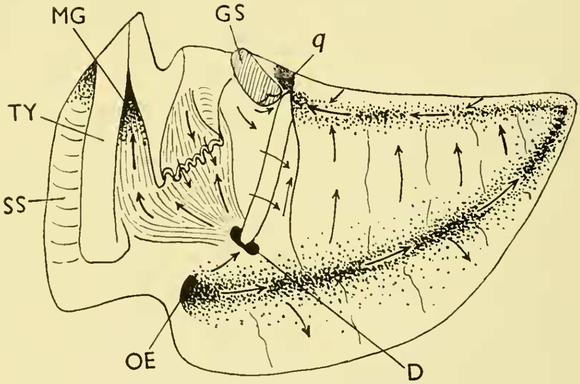

Figure 6. *Hipponix antiquatus*, stomach opened along dorsal surface, showing appearance in life. ×10. *D*, opening of duct into digestive diverticula (ventral); *MG*, opening into mid-gut (dorsal) separated by typhlosole (*TY*) from style-sac (*SS*); *OE*, opening of oesophagus (ventral). *q*, *q*, material accumulated by ciliary currents at side of gastric shield (*GS*) where normally caught up by the substance of the revolving head of the style.

extends to the right. The walls of this appear corrugated when the stomach is opened, ciliation is poorly developed but there is evidence of muscular contraction, sections revealing the presence of some strands of muscle around this region of the stomach.

The digestive diverticula form a compact mass on the ventral side of the stomach as shown in figures 2 and 5 (DD). The tubules contain many dark spherules (seen in the section shown in fig. 5) which are probably of an excretory nature. Owing to their presence the diverticula form a black mass when viewed from the ventral side (fig. 2). Among the tubules and around the gut generally there is abundance of a yellow, vesicular connective tissue. The mid-gut and rectum extend forward in the roof of the mantle cavity where they form a series of loops (fig. 3, MG and R). In an animal with a shell diameter of 12 mm. these terminal regions of the gut pulled out to a length of some 22 mm.

Food and Feeding

The only previous account of feeding in *Hipponix* appears to be that of Risbec (1935) on *H. australis*. This species lives on the shells of other gastropods, usually of species of *Turbo*, and characteristically near to the exhalant aperture. So situated, it feeds on the faecal pellets of the "host," the terminal processes of the proboscis separating and then coming together rapidly when the relatively enormous food masses are swallowed. *Hipponix antiquatus* feeds in essentially the same manner but on fragments of material—organic detritus, pieces of algae, etc.—that are carried within the very limited area in front of the shell where alone the proboscis can browse. In the absence of automatic supplies of food, such as those received by *H. australis* from the animal it lives upon, this type of feeding can only be carried on by a sedentary animal if food supplies are constantly being renewed by water movements.

The proboscis itself is muscular and very active. The terminal lobes, with the mouth which they flank, were frequently seen to open widely and grope forward in apparent search for food. The odontophore was then seen to protrude from the mouth opening. Somewhat similar observations were made on *C. ungaricus* after mucus-laden food masses had been carried on to the surface of the propodium (Yonge, 1938). In this species, however, the proboscis, which is grooved anteriorly, represents the much extended terminal lobes in *Hipponix*. How widely the mouth must dilate in *H. antiquatus* is indicated by the nature of the stomach contents. These, together with much amorphous matter, probably organic detritus, comprise sand grains and also fragments of calcareous coralline algae up to 2 mm. long and 0.5 mm. wide. The radula must convey these fragments into the buccal mass and anterior oesophagus the powerful ciliation of which, possibly aided by some muscular action, serving to carry them into the stomach.

Within the stomach material would appear initially to pass to the right, into the caecal extension, as indicated in figure 6. This serves as a store and perhaps to some extent also as a gizzard although the trituration which must occur before the larger particles can pass into the mid-gut is probably completed by the action of the style and gastric shield. Certainly particles are carried to the edge of the gastric shield (fig. 6, *q*) where, in the intact stomach, they will be caught up in the head of the rotating style. Fine particles only will finally be carried into the large duct (D) leading into the digestive diverticula; the greater part of the stomach contents must pass, essentially unchanged apart from digestion of starch and some trituration, into the mid-gut. A very similar type of stomach, with a large caecal extension, is described by Graham (1939) in *Pomatias (Cyclostoma) elegans.*

Within the mid-gut the faecal material becomes firmly compacted into pellets of relatively enormous size. Each is oval in shape and from 700 to 800 μ long and about 500 μ in diameter. When crushed they are found to consist of fine amorphous material, dark green in colour with fine fragments of lime and silica. These pellets may occur in multiple rows and in such numbers as to distend the mid-gut and rectum to as much as three times the normal diameter. Indeed the roof of the mantle cavity may be largely occupied by as many as 16–20 of these pellets within the coilings of the mid-gut and rectum. The anal opening, normally small, is greatly distended at defecation. The exhalant current must aid in carrying the pellets clear of the shell where water movements may dispose of them. In the quiet water of an aquarium tank the pellets were deposited in large numbers just outside the margin of the shell. Under these conditions they might possibly be seized by the groping proboscis and swallowed.

There is no evidence of any discrimination in feeding. Anything that is available, up to a relatively very large size, appears to be swallowed. The oesophagus is wide enough to permit the passage of, and the stomach capacious enough to store, large particles. The stomach is that typical of a style-bearing gastropod, as summarized by Graham (1939), permitting (1) mixing of food with the style substance, (2) sorting of fine particles for passage into the digestive diverticula, (3) removal of larger particles and waste from the digestive diverticula into the mid-gut, (4) rotation and passage into the stomach of the style. The very great amount of indigestible matter in the food is accumulated into exceptionally large faecal pellets which cannot cause fouling of the mantle cavity.

REPRODUCTIVE ORGANS

Every specimen examined in life or dissected was female. One small specimen of which longitudinal sections were made showed no sign of reproductive organs and was presumably immature. The related *Capulus ungaricus* is a protandrous hermaphrodite (Giese, 1915) and this must surely also be true for *Hipponix*.* In *C. ungaricus* the reproductive system is simple, consisting, in the male phase, of a testis with associated ampullae and a duct leading into a pouch with which a receptaculum communicates by a fine duct. The male genital opening lies at the side of the right shell muscle and the sperm is carried by way of a ciliated groove to the tip of a simple penis which is without glands. After sex change, the gonad enlarges to form an ovary without ampullae, the pouch of the male phase now becomes what Giese describes as a uterus into which the receptaculum continues to open. The sperm groove and the penis disappear but the female reproductive aperture, although longer, remains in the original position.

Presumably the males, being younger and probably more active, are able to move on to and copulate with the larger and probably completely immobile females. Jones (1949) describes the presence of small specimens of *C. ungaricus* on the shells of larger ones, and these may well have been males and females respectively. After copulation, sperms would presumably be stored in the receptaculum and later fertilize the eggs when they entered the "uterus." The latter is thick-walled and glandular and responsible for the formation of the protective capsule discussed in the next section.

The small specimen of *H. antiquatus* without reproductive organs was some 6 mm. in diameter and was attached to rock. If this animal was indeed immature and if all members of this species are protandric hermaphrodites then they cannot be mobile in a subsequent male phase. Certainly no small mobile individuals were observed and in the very turbulent conditions where *H. antiquatus* lives, permanent attachment in early life would seem to be almost essential. This matter cannot be regarded as settled but all available evidence, admittedly very limited, indicates that the species, almost certainly a protandric hermaphrodite, is not mobile in the male phase and so copulation cannot occur. If this be so, then fertilization may occur in one of two ways.

The first possibility is that the spermatazoa are liberated freely into the sea and that fertilization occurs after these have been carried into the mantle cavity and have entered the genital aperture of a female. Such "current fertilization" is known to occur in *Turritella communis*

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*The parasitic *Thyca stellasteris*, according to Koehler and Vaney (1912), is not hermaphrodite although the male is smaller than the female.

(Fretter, 1946) and in various members of the Vermetidae (Morton, 1951*b*). All of these animals are, however, ciliary feeders (Graham, 1938, Morton, 1951) and so with enlarged ctenidia which create a powerful inhalant current. In addition the pallial genital duct is widely open ventrally to permit the reception of sperm carried to it in the water. All of these animals, moreover, probably live in numbers together and in comparatively still water, i.e. under conditions where a local concentration of sperm adequate to ensure fertilization could be produced. In *Hipponix* the inhalant current is much weaker, the concentration of animals is less while the water movements seem normally far too great to allow any effective concentration of sperm. Further, the very short pallial oviduct in *Hipponix* does not provide the facilities for entrance of water-borne sperm that are present in *Turritella* and the vermetids.

The other alternative is that sperm produced during the male phase are stored for subsequent fertilization of eggs produced by the *same animal* when it passes into the female phase. This would not be unprecedented in the Mollusca, having been shown to occur in the wood-boring lamellibranch, *Xylophaga dorsalis* (Purchon, 1941). This animal alternates in sex but the sperms produced in a male phase are stored in a receptaculum for use in the subsequent female phase. *Xylophaga dorsalis* lives largely isolated in drift wood and this is probably the only feasible method by which fertilization can be assured. Although the habitat is different, the problem in the case of *H. antiquatus* is not dissimilar and the solution may be the same.

The female reproductive organs are very similar to those described by Giese in *Capulus*. They are situated on the extreme right side of the visceral mass and consist of an ovary and, to employ the terms used by Fretter (1946), a gonadial duct (incorporating renal constituents), and a wide pallial region (fig. 7, OD) forming a capsule gland into which opens, by a narrow duct posteriorly (fig. 7**B**, RS), a rounded receptaculum seminis. In section sperm were seen within this organ. The eggs are large, containing great quantities of yolk, when they leave the ovary (fig. 7**C**, OV) and there is no evidence of any albumen gland. A capsule is almost certainly laid down around each egg, after fertilization by sperm from the receptaculum, by the conspicuously thick and glandular walls of the capsule gland (uterus of Giese). In this state the eggs will be passed into the mantle cavity.

Attachment of Egg Capsules

Sedentary Mesogastropoda must either attach the egg capsules to the inside of the shell, as do the Vermetidae (Morton, 1951*b*), fasten them

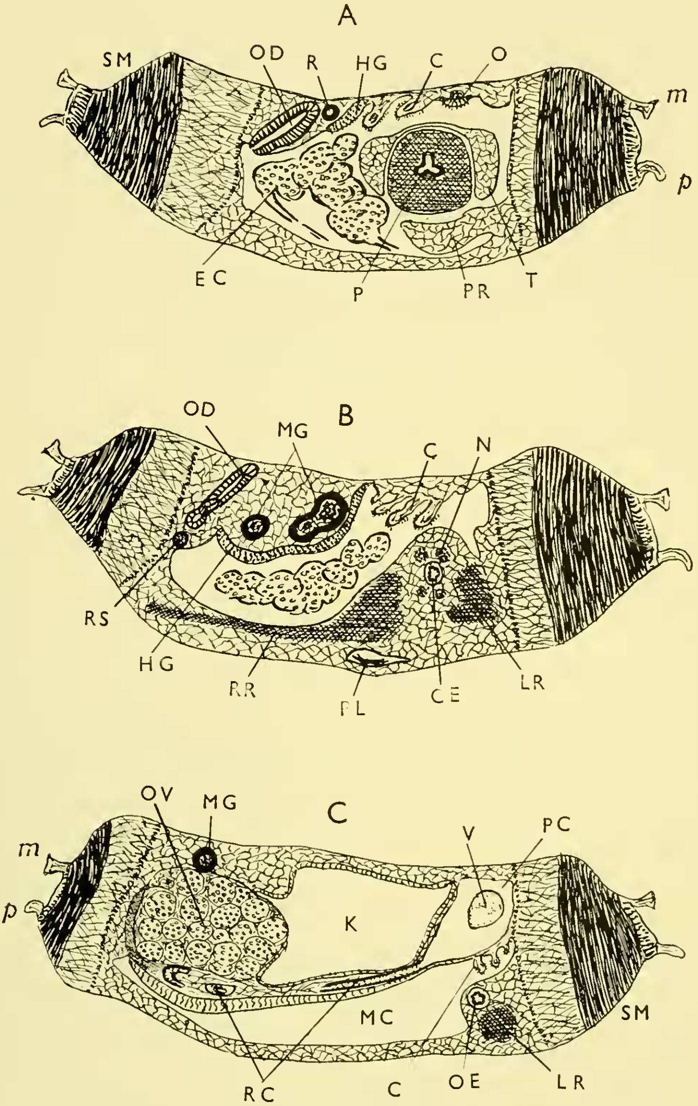

Figure 7. *Hipponix antiquatus*, transverse section through the anterior (**A**), middle (**B**), and posterior (**C**) regions of the mantle cavity. ×5. *EC*, egg capsules; *N*, nerve collar at base of proboscis; *OV*, ovary containing large, yolk-filled eggs; *RC*, reno-pericardial canal, showing opening into pericardium (*PC*); *RS*, duct from oviduct (capsule gland) into receptaculum seminis; *T*, tentacle; *V*, ventricle. Other lettering as before.

to the rock or pebbles on which the female rests, as in Calyptraeidae such as *Crepidula fornicata* (Lebour, 1937), or else retain them secured to the actual body of the female. This is the case in both *Capulus* and *Hipponix*. In *C. ungaricus* a single large egg capsule or cocoon is attached to the large propodium of the female. Full references to literature are given by Thorson (1946) who summarizes previous work in the statement that "Each female protects a single thin-walled cocoon of the form of a sausage, and each cocoon contains several eggs, 200 μ across, which hatch as veligers through a fissure on the under side of the cocoon."

Although Risbec (1935) does not mention males and gives a very imperfect account of the female genital system in *H. australis*, he gives a good description of the egg capsules in this species. He notes that it is impossible to observe egg-laying and the process of formation and attachment of the capsules. This is equally true for *H. antiquatus*. He describes the presence of six or more capsules each containing a number of eggs and attached by a slender stem to a plate which is itself imbedded in the tissues of the foot. He considered that these sacs received the eggs and also yellow nutritive material of a fatty nature. He was unable to observe the role of the foot in the formation and attachment of these capsules.

Conditions are essentially similar in *H. antiquatus*. After the completion of egg-laying the mantle cavity of the female is completely filled by from six to eight egg capsules each containing up to 50 yellowish eggs. The eggs measured about 350 μ in diameter, the greatest transverse diameter of the capsules being 840 μ. Each capsule was, as in *H. australis*, attached by an attenuated stalk to a perforated calcareous plate which in turn was attached within a membranous area situated in the depression ventral of the propodium (figs. 4, **7C**, and 8; PL). As shown in figure 8, the capsules usually bulge forward so that they may project a little distance out of the mantle cavity (at least when the animals have been detached). The head is pushed over to the left of the mantle cavity and the animal must have some difficulty in maintaining the necessary circulation of water through the mantle cavity.

Unfortunately, it was impossible to observe the mode of formation and attachment of the egg capsules. Owing to the sedentary habit of this animal, full details of this process could probably only be made out by examining great numbers of animals during the period of egg-laying in hope of obtaining animals in all stages. The first egg-carrying female was obtained on April 5; during the summer all animals had egg capsules although some of these were empty.

It is, however, certain that the eggs are large and yolky when they leave the ovary, where they were observed in sections (fig. **7C**, OV). After

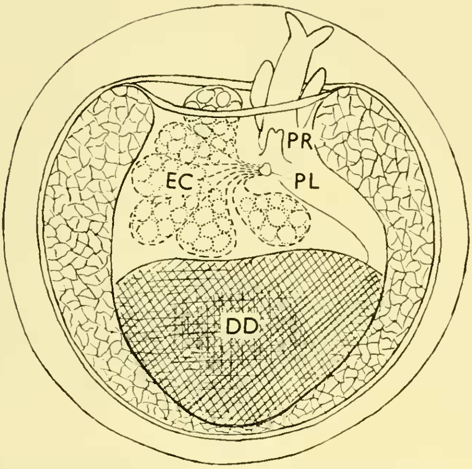

Figure 8. *Hipponix antiquatus*, ventral aspect with egg capsules in the mantle cavity. ×5. Lettering as before.

fertilization they presumably each receive a protective covering while in the capsule gland. It is, however, likely that the large capsules, each containing many eggs, are secreted by the gland that opens on the dorsal surface of the foot and which is certainly active, judging from sections, at this time. Moreover, it has been shown by Werner (1948) that, in *Crepidula fornicata*, a stalked capsule is secreted around the eggs by such a gland in the propodium. The calcareous plate and its investing membrane may be formed within the pocket ventral to the propodium; sections show evidence that the epithelium has secreted this membrane. But it is not advisable to speculate further on a matter that can only be determined by observation.

So far as could be determined, all eggs developed. There was no evidence that any of them formed food for others or that the capsules contained any additional nutritive material as suggested by Risbee. The embryos develop into fully shelled larvae but whether these actually crawl away after emergence from the capsules, as described by Risbee for *H. australis*, was not seen. In view of the very specialized habitat, it is more than probable that, in *H. antiquatus* also, the young crawl away from the parent to settle in due course permanently on the adjacent rock surface.

Discussion

Gastropods which possess the limpet form and the accompanying habit of life are particularly well fitted for survival on a hard substratum in the turbulence of the intertidal or shallow waters where such substrata normally occur. It is therefore not surprising that the limpet form, with its secondary symmetry (see Yonge, 1947, p. 490, fig. 31) has independently been evolved on a number of occasions. The particular conditions that exist in *Hipponix* are most suitably discussed by comparing them with those found in examples of the other chief types of marine limpets.

In figure 9 comparison is made between four types of limpets, (**A**) *Diodora (Fissurella)* and (**B**) *Acmaea* are both archaeogastropod limpets the former having paired, i.e. zygobranchous, aspidobranchiate ctenidia, the latter having a single aspidobranch ctenidium. (**C**) *Hipponix* is a mesogastropod limpet with a pectinibranch ctenidium and (**D**) *Siphonaria* is a pulmonate with a secondary gill in what has been a pulmonary mantle cavity. A cap-like shell and a horseshoe-shaped shell muscle (with the

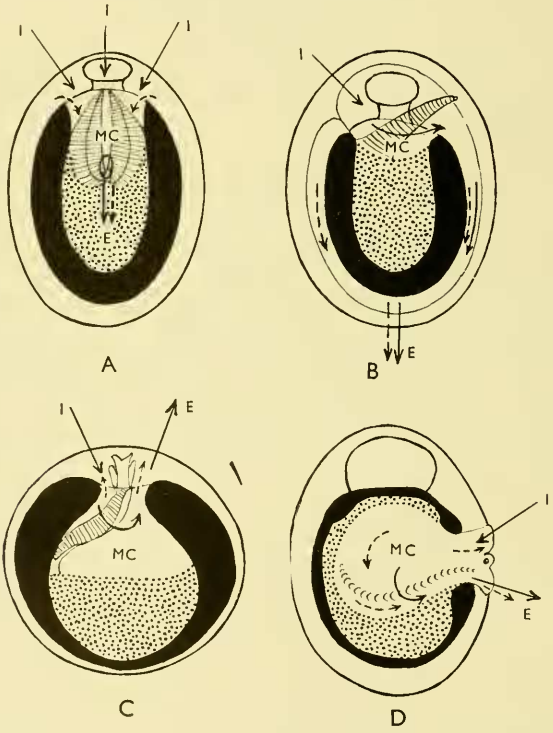

Figure 9. Diagrammatic comparison, from dorsal aspect, of four types of limpets, showing mantle cavity (*MC*) with inhalant (*I*), exhalant (*E*) and major cleansing currents (latter broken arrows), also shell muscles (black) and visceral mass (stippled). **A**, *Diodora* (Archaeogastropoda, Fissurellidae) with paired and symmetrical ctenidia, exhalant current dorsal; **B**, *Acmaea* (Archaeogastropoda, Patellacea) with single aspidobranch ctenidium, exhalant current posterior; **C**, *Hipponix* (Mesogastropoda) with pectinibranch ctenidium, exhalant current anterior; **D**, *Siphonaria* (Pulmonata) secondary gill, exhalant current on right.

opening on the right in *Siphonaria*) are common to all. The course of the respiratory and cleansing currents may be briefly summarized. The anterior mantle cavity of the prosobranchs (**A–C**) has a generalized anterior inhalant current (I) in **A** but, with the loss of the right ctenidium, this is confined to the left in **B** and **C**. In **A** the exhalant current (E) issues dorsally, through the shell aperture found in all zygobranchous gastropods and here apical in position, in **B** it is carried by way of the right pallial groove to the posterior end of the animal, whence also passes sediment collected in the mantle (nuchal) cavity and in the pallial grooves. From such a condition have been derived those in the more specialized *Lottia*, *Patina*, and *Patella* (Yonge, 1947) with their secondary pallial gills. These Patellacea (Docoglossa) represent the most successful of all limpets and this may well be associated with the use they, alone among limpets, have made of the pallial grooves. In *Hipponix* (**C**), apart from the flattening already discussed, the mantle cavity and its currents are those of a typical pectinibranch. In **D** the pulmonate mantle cavity has been successfully readapted for aquatic life by the appearance of secondary gills within this (Yonge, 1952) and *not* in the pallial grooves. The restricted opening of the mantle cavity on the right side is retained with the exhalant current issuing immediately posterior to the inhalant opening.

It is in the matter of feeding that *Hipponix*, and the mesogastropod limpets in general, differ from these archaeogastropod and pulmonate limpets. The latter all browse on encrusting vegetation, moving very slowly over the rock and scraping this with the broad radula. The mesogastropod limpets may be divided into (1) those in which the ctenidial filaments have been greatly elongated and which feed exclusively by ciliary currents, i.e. *Crepidula* and *Calyptraea* (Calyptraeidae) and (2) those in which there is a pronounced proboscis. In both groups the power of movement is lost, effectively even where the animal does not actually become attached. In the Calytraeidae movement ceases to be necessary because food, suspended in the inhalant current, is brought to the animal. But in the second group a most interesting variety of conditions prevails.

In *Capulus*, which is the least specialized, the grooved proboscis, formed by prolongation of the terminal lobes in *Hipponix*, may be used to take in food collected by the enlarged ctenidia (Yonge, 1938) but it may probably be also used to take in material similarly collected by a lamellibranch (Orton, 1949). In both *Hipponix australis* and *H. antiquatus* the ctenidium is not concerned with feeding, the proboscis swallowing relatively large food masses. In the former species, which lives on a "host" animal, the habit has resemblance to that described by Orton for *C. ungaricus*, but *H. antiquatus* is not dependent on any other animal. Although cemented to the substratum, yet it uses the proboscis to collect food in front of the shell. Species of a third genus, *Thyca*, have also lost the power of movement but in association with a completely parasitic life. They are ectoparasitic on echinoderms, the foot being reduced but the long proboscis penetrating deep into the tissues of the host (Schepman and Nierstrasz, 1909; Koehler and Vaney, 1912). The disc of attachment is formed by the proboscis, the columellar muscle described by Koehler and Vaney apparently consisting of the retractor muscles of the head.

In *H. antiquatus* the three most striking characteristics are (1) the flattening of the shell, with its consequences on the form of the mantle cavity and the disposition of the head, (2) cementation to the substratum by the secretion of a ventral "valve" by the undersurface of the foot and with consequent loss of motility, and (3) feeding, while so attached, by means of the proboscis. All three, however, are related to one another and to the habitat. A much flattened limpet which was cemented to the substratum would have survival value under the conditions where *H. antiquatus* lives, namely within crevices among rocks exposed to the full and almost unvarying force of the Pacific surf. Under such conditions food will constantly be renewed so that exclusive dependence on the proboscis is possible. This is not the case in *C. ungaricus* which lives, sublittorally, in very much quieter water.

Again, members of both of these groups of limpets are protandrous hermaphrodites (certainly *Crepidula* and *Calyptraea*, also *Capulus* and almost certainly *Hipponix*) but have the typical female genital system of the mesogastropods with large and internally fertilized eggs. The egg capsules must of necessity be attached either to the underlying substratum or to the animal itself. Only the latter is possible in *Hipponix* because the animal is cemented. The precise period at which the sperm enters the receptaculum, which involves the question of whether self or cross fertilization occurs, remains to be determined, as does the precise manner in which the egg capsules are attached to the underside of the propodium.

There is finally the question of classification. Thiele (1931) places *Amalthea (=Hipponix)* in the Amaltheacea but *Capulus* and *Thyca* in the family Calyptraeidae. While there is certainly much still to be learned about these and allied genera and families, there can be no doubt that *Hipponix* is much more closely allied to *Capulus* than would appear from Thiele's classification, which cannot in this particular instance be supported. The precise position of *Thyca*, so greatly modified in form and habit and yet not a protandrous hermaphrodite, appears to need further scrutiny.

SUMMARY

Hipponix antiquatus is a mesogastropod limpet of particular interest owing to its sedentary habits. It lives cemented to the substratum in crevices among rocks often fully exposed to the Pacific surf. It is highly adapted for life in such an extreme habitat.

The ventral surface of the foot secretes a "ventral valve" closely resembling the "dorsal valve," i.e. shell, secreted by the mantle. The margins of the two make perfect contact when the horseshoe-shaped shell muscle contracts.

The opening of the mantle cavity is constricted causing displacement dorsally of anus and ctenidium; the shell is also much flattened with consequent effects on the mantle cavity and displacement to the left of the head. In other respects the disposition of the pallial organs is that typical of mesogastropods.

The ctenidia are solely concerned with respiration. Feeding is by means of a muscular proboscis which is extruded from the mantle cavity and swallows relatively very large masses of organic detritus, such as fragments of calcareous algae.

The alimentary canal is modified for the reception and utilization of such food masses. The stomach is large but otherwise that typical of a style-bearing mesogastropod. There is a single opening into the ventrally disposed digestive diverticula. Faecel pellets are exceptionally large.

Available evidence indicates that *H. antiquatus*, like the allied *Capulus ungaricus*, is a protandric hermaphrodite. Owing to the sedentary habit and to the rough water in which it lives, cross fertilization may be impossible and it appears more probable that spermatozoa produced during the male phase are stored in the receptaculum for fertilization of eggs produced in the subsequent female phase.

Large egg capsules, each containing a number of large, yolky eggs, are attached to a calcareous plate embedded ventral to the propodium. The mantle cavity is largely filled by these capsules during spring and early summer.

In comparison with archaeogastropod and also pulmonate marine limpets, mesogastropod limpets are sedentary, feeding by means of ciliary currents (*Crepidula*, *Calytraea*, *Capulus*) or by means of a proboscis either on organic detritus or faeces (*Hipponix* spp.) or else parasitically (*Thyca*). With the exception of *Thyca*, all of these limpets are also protandric hermaphrodites.

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